

Touch and the Body: The Role of the Somatosensory Cortex in Tactile Awareness

Abstract

This review addresses the role of early sensory areas in the awareness of tactile information in humans. The results of recent studies dealing with this important topic are critically discussed: In particular, we report on evidence from neuropsychology, neurophysiology, neuroimaging, and behavioral experiments that have highlighted the crucial role played by the primary somatosensory cortex (SI) in mediating our awareness of tactile information. Phenomena, such as tactile hallucinations, tactile illusions, the perception of supernumerary limbs, and synaesthesia are also discussed. The research reviewed here clearly shows that the activation of SI is necessary, but not sufficient, for the awareness of touch. On the basis of the evidence outlined here, we propose a neurocognitive model that provides a conceptual framework in which to interpret the results of the literature regarding tactile consciousness.

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"everything occurs on the skin" (Helmholtz, 1821-1894).

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Theoretical Framework

Traditionally, studies of the awareness of sensory information in humans have focused on visual awareness (e.g., Baars, 1997; Singer, 1998; VanRullen & Koch, 2003). This is rather surprising when one considers that touch, the first sense to develop in the womb in humans, might be the matrix upon which the awareness of ourselves as individuals, separated from the external world, starts to form (e.g., Barnett, 1972; Gottlieb, 1971; cf. Bermudez, Marcel, & Eilan, 1995; Montagu, 1978).

Our awareness of touch needs to incorporate the stimulation of a much larger receptor surface as compared to vision (see Montagu, 1971). It has been estimated that our skin and its tactile receptors account for 18% of our body mass (e.g., Montagu, 1971). The sense of touch continuously informs our consciousness about areas of the body that are currently out of view (i.e., a person's back) and, in contrast with vision, it can do this regardless of the position or status of our head or eyes. As far as this point is concerned, one cannot fail to note that we can close our eyes and prevent visual stimuli from entering consciousness, but perhaps as an ultimate form of bodily protection against injury, we can never voluntarily shut down our sense of touch (see Gregory, 1967; though see Marx et al., 2003, for evidence that the overall neural level of activation in the somatosensory system varies as a function of whether the eyes are open or closed). It is for reasons such as these that developing an understanding of how our awareness of tactile sensations comes about should be considered of great importance.

If one considers the number of differences between the processing of tactile and visual information, one might reasonably expect there to be differences in terms of the mechanisms underlying the awareness in these two sensory modalities. Indeed, although vision is the last of our senses to develop, by the time we reach adulthood, nearly half of the cerebral cortex (i.e., the outer layer) of the brain is involved in some way or other in the processing of visual information (Sereno et al., 1995). Certainly, it is only via the study of tactile awareness that we can hope to understand whether or not touch and vision differ in terms of the cognitive and neural mechanisms leading to conscious sensations.

There are, however, a number of important reasons why the awareness of tactile information has thus far received far less attention than the same topic in other sensory modalities (especially with respect to vision). The first reason is mainly philosophical. After Aristotle and Plato, vision has always, with very few exceptions (e.g., Berkeley, 1732), been considered the most important of the human senses (see Classen, 1997). The greater importance given by philosophers to the study of visual awareness seems to be, at least in part, related to the historical discussion regarding the relationship between "appearance" and "reality". In fact, a number of epistemological scenarios have been designed across the centuries in order to understand the nature of these two concepts (e.g., Pastore, 1971). From a more empirical point of view, this might also be related to the fact that vision typically "dominates" or "captures" touch when the two modalities conflict (e.g., see Bertelson & de Gelder 2004; Rock & Harris, 1967, for reviews; though see Heller, 1992).

The second reason is that touch is often considered to represent a rather complex sensory modality, even though it is considered to be a "primitive" sense (e.g., Gregory, 1967). In fact, what we commonly call the sense of touch, actually

comprises the processing of pressure, temperature, pleasure, pain, joint position, muscle sense, and movement (see Berkley & Hubscher, 1995; Iggo, 1977; Löken, Wessberg, Morrison, McGlone, & Olausson, 2009; Lumpkin & Caterina, 2007; Olausson et al., 2008; Rolls et al., 2003; Spence, Bentley, Phillips, McGlone, & Jones, 2002). Whether pain should be considered to be part of the sense of touch is still a matter of some debate (e.g., Berkley & Hubscher, 1995). Currently, there is also little agreement as to whether all of the other forms of processing should be considered to be separate sensory modalities or sub-modalities of touch (see Auvray, Myin, & Spence, 2010; Durie, 2005). This latter point may be less relevant, considering that visual information has also been shown to be analyzed by a different subset of processing systems (e.g., those involved in color, movement, and orientation perception) and receptors (e.g., rods, cones and photoreceptors; see Zeki, 1993, for a review).

A third reason is related to the difficulties associated with designing experiments to study touch empirically. This is, in part, also due to the lack of proper technological devices for delivering controlled and reliable tactile stimuli (see Ingeholm et al., 2006). To a certain extent, the latter point has been addressed by recent technological advances, making the experimental study of touch somewhat less challenging than it used to be (see Gallace, Tan, & Spence, 2007).

A final reason for the lack of attention given by researchers to the neural and cognitive mechanisms of tactile awareness is related to the lack of a proper language to classify tactile/haptic sensations (see Spence & Gallace, 2008, for a discussion on this point). Although the contents of visual awareness can easily be discussed, it is rather difficult to discuss the contents of tactile consciousness if we lack a shared vocabulary for talking about touch, and the contents of tactile consciousness. This latter point, unfortunately, still remains valid, although a few attempts have recently been made to develop a lexicon for touch (see Sonneveld, 2007, cited in Sonneveld & Schifferstein, 2008).

In the last few decades, we have seen a number of studies that have tried to investigate the role of primary sensory areas in the awareness of visual information (e.g., Cowey & Walsh, 2000; Kleiser, Wittsack, Niedeggen, Goebel, & Stoerig, 2001; Lamme, 2001, 2006; Lamme, Supèr, Landman, Roelfsema, & Spekreijse, 2000; Lee & Blake, 2002; see Rees, 2007; Tong, 2003, for reviews). The results of these studies indicate that neural activation across early sensory areas (such as V1) is not in-and-of-itself sufficient to elicit awareness. By contrast, whether or not V1 is necessary to elicit visual awareness of incoming visual stimuli is currently still a somewhat controversial topic (e.g., Kleiser et al., 2001; Lamme et al., 2000; see also Rees, 2007).

Perhaps because of the reasons listed above, the role of sensory areas, specifically of the somatosensory cortex in people's awareness of incoming tactile information, has only relatively recently been addressed by cognitive neuroscientists (e.g., Palva, Linkenkaer-Hansen, Näätänen, & Palva, 2005; Preissl et al., 2001; though see Libet, Alberts, Wright, & Feinstein, 1967; Head & Holmes, 1911, for early studies; see Gallace & Spence, 2008). The present review aims to discuss the results of those studies that have addressed this topic. Given the close relationship that has been highlighted between the sense of touch and the representation of the body (e.g., Haggard, Taylor-Clarke, & Kennett, 2003; Knoblich, Thornton, Grosjean, & Shiffrar, 2006), we decided to give more visibility in the present review to those studies where

this important link can be stressed. By contrast, although a large body of research has dealt with topics related to awareness of pain and body representation (e.g., Moseley, 2004, 2005; Moseley, Parsons, & Spence, 2008), we will not discuss the extensive body of literature surrounding this topic here.

In this review of the literature, we start by describing the anatomical organization of the somatosensory cortex and its connectivity with other brain areas. By doing so, we define some of the key aspects of the neural information processing of tactile information that will become useful later when trying to understand the results of both behavioral and psychophysiological studies relevant to the awareness of touch. Next, we report the results of those neuroimaging and neuropsychological studies that have investigated the role of the somatosensory cortex in mediating the awareness of tactile information. Taken together, these studies highlight the importance of the somatosensory cortex for our awareness of the body and the tactile sensations occurring across its surface. We will also critically discuss classic (at least in the extant visual literature; e.g., Kim & Blake, 2005) topics strictly related to awareness of information such as synaesthetic tactile perceptions, tactile illusions, and hallucinations, and their neural basis. Next, we report recent research showing that the activation of the somatosensory cortex by itself cannot support the awareness of touch. Finally, we propose a model for the awareness of touch that is consistent with the findings reported in the literature. Although the emphasis will be squarely on human research whenever possible, we will report the results of both animal and human studies. The words *tactile awareness*, unless otherwise stated, will be used to describe both active (haptic) and passive touch, although most of the literature reported concentrates on passive tactile sensations. Finally, this review will not deal directly with people's awareness of their bodies, of their movement, and/or of their posture (i.e., proprioception and enteroception; see Craig, 2002), although these topics will be discussed where relevant to the main themes of the review.

In the present manuscript we will consider *tactile consciousness* in terms of “the content of a neural representation (see deCharms & Zador, 2000, for the concept of neural representation as it is considered in the present manuscript) that concerns a given information, of becoming available for explicit report” (see Dehaene & Changeux, 2003; Weiskrantz, 1997; see also Gallace & Spence, 2008, for a similar definition). The terms *tactile awareness*, *awareness of touch*, and *awareness of tactile information* will be used interchangeably in this review with the same meaning. It is worth noting that the definition used here implies that we are primarily dealing with *access consciousness* rather than with *phenomenal consciousness* (see Block, 1995, on this point). On the basis of this definition, when we refer to tactile awareness, we are referring to those aspects of the neural activity elicited by the presentation of tactile stimuli (i.e., any physical stimulus that gives rise to activation of at least one class of sensory receptors located in the dermis) on the participants' sensory receptive surface that can be reported explicitly (and in this case, the terms awareness of tactile sensations/tactile stimulation/touch will be used). We also will consider those conditions in which a given tactile sensation, similar to that elicited by the actual presentation of tactile stimuli on the skin, can be explicitly reported by participants, despite the fact that no actual stimulation was present (hence including tactile illusions and delusions). Note that in the latter case the individual is aware of internal states elicited by internal causal conditions. The terms *conscious information processing* will be used in order to describe those cognitive and neural mechanisms responsible for the explicit report of tactile information (no matter whether any actual

tactile stimulation occurred or not). It is finally worth highlighting here that the present review will discuss those conditions responsible to attribute consciousness to *creatures' states* (neurobiological and representational) and not to creatures themselves (see Manson, 2000, for a discussion regarding the distinction between *state consciousness* and *creature consciousness*).

In this review, we demonstrate that early sensory processing areas, such as the primary somatosensory cortex (S1), are of great importance for eliciting an awareness of tactile information, especially given their involvement in the conscious experience of the body and of its modulation. As has been suggested elsewhere with regard to the awareness of visual information (e.g., Kleiser et al., 2001; Rees, 2007), however, the activation of higher order processing areas is also needed for an awareness of touch. That is, the activation of S1 appears to be a necessary, but not sufficient, condition for our consciousness of touch.

The Organization of Somatosensory Cortex

In defining the role of somatosensory cortex in mediating our awareness of tactile sensations, it is important to describe the neural organization of this system and its connections with other brain areas. We believe that it is mainly from the reciprocal interactions between the somatosensory cortex and other brain areas that an awareness of tactile information arises: There isn't a single brain area that is responsible for the awareness of information (i.e., an area that is activated only when people become aware of tactile stimuli). The circuit responsible for awareness of information is the same as that involved in the initial processing of that information. Specifically, in our view, tactile consciousness results from the activation of a circuit comprising many different neural structures that are connected, either directly or indirectly, to S1. Here we try to analyze the organization and connections of the components upon which such a circuit is based (see also Dijkerman & de Haan, 2007, for a recent review).

Stimuli, presented to just one side of the body (unilateral sensory stimuli) from the sensory receptors distributed across the body surface, are transmitted either by the primary afferent fibers of dorsal root ganglia, or by the trigeminal sensory neurons, to the ventral posterior lateral and medial nuclei of the thalamus. From there, the majority project to the contralateral primary somatosensory cortex (e.g., Blatow et al., 2007; Gardner & Kandel, 2000; Jones, 1986). The primary somatosensory cortex (S1) comprises Brodmann's areas 3a, 3b, 1, and 2 (in this rostro-caudal order), and it is located in the post-central gyrus of the brain. S1 is involved in the central processing of both tactile and nociceptive stimuli (e.g., Kaas 1990; Kenshalo & Willis, 1991; see Figure 1).

Animal studies have shown that neurons within each cortical site in S1 (particularly those in layer IV) are arranged in columns that represent specific regions of the body (note that a similar columnar organization also characterizes the neural map present in human area VI; e.g., Hubel & Wiesel, 1962; Mountcastle, 1957; see Swindale, 2001, for a discussion on the concept of *cortical maps* among the different senses). This observation has also been confirmed in humans by direct stimulation of the brain in awake patients just before they undergo surgery. Specifically, it has been shown that the organization of S1 is somatotopic (e.g., Penfield & Boldrey, 1937; Penfield & Rasmussen, 1950): The stimulation of different regions of S1 can elicit tactile sensations that are explicitly referred to specific parts of the body (see Figure 1). As a consequence, a complete map of the body surface can be detected on S1; this is known as the *somatosensory homunculus* (e.g., Narici et al., 1991; Penfield &

Boldrey, 1937; Penfield & Rasmussen, 1950). Interestingly, the relative size of the different portions of SI representing different body parts, is not a function of the size of the represented body part itself, but rather of the sensitivity to tactile stimuli in that area (as also determined by the density of the afferent fibers that innervate it). For example, a relatively larger proportion of the somatosensory cortex is given over to the representation of the hands and lips than to other parts of the body given their relative surface area (e.g., Nakamura et al., 1998; Narici et al., 1991; Penfield & Boldrey, 1937).

A)

B)

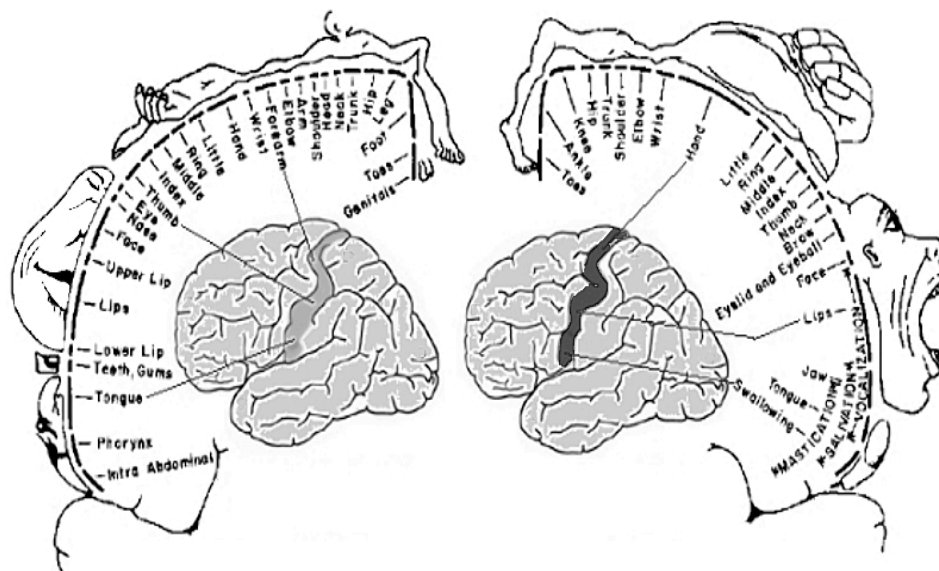


Figure 1. Somatotopic map of the body in the pre- and post-central gyrus of the brain (see Penfield & Rasmussen, 1950). A) Somatosensory homunculus; B) Motor homunculus.

It is important to note that the organization of the somatosensory map in SI is similar to another somatotopic map, the *motor homunculus* found in the precentral gyrus (e.g., Penfield & Rasmussen, 1950). The close somatotopic correspondence between these two maps highlights the important relationship between touch and movement (see Gallace & Spence, 2008; see Figure 1). For example, the areas responsible for the perception of touch on the hands in the somatosensory homunculus are located mostly in front of the areas responsible for hand movements in the motor homunculus. Indirect confirmation of the latter claim comes from Wilder Penfield's original studies (e.g., Penfield & Boldrey, 1937; Penfield & Jasper, 1957; Penfield & Rasmussen, 1950). Indeed, Penfield and his colleagues reported that at ~25% of somatosensory and motor cortical sites, movements and tactile sensations were produced, respectively, by means of direct stimulation of the brain, suggesting once again the existence of close somato-motor functional relationships.

The secondary somatosensory cortex (SII) is adjacent to SI. This area is reciprocally connected with ipsilateral SI via corticocortical connections (e.g., Burton, 1986; Gardner & Kandel, 2000; Jones, 1986). Evidence from several mammalian species, including non-human primates, suggests the presence of direct thalamocortical projections to SII (e.g., Chakrabarti & Alloway, 2006; Kwegyir-Afful & Keller, 2004; Murray et al., 1992; Turman et al., 1992; Zhang et al., 2001). Animal

studies have shown that left and right SII cortices have reciprocal connections and the majority of SII neurons display bilateral receptive fields (RFs; e.g., Burton, 1986; Caminiti et al., 1979; Innocenti et al., 1974; Jones, 1986; Manzoni et al., 1989). Furthermore, SII is reciprocally and somatotopically connected to contralateral SI (e.g., Barba, Frot, & Mauguiere, 2002; Jones, 1986; Manzoni et al., 1986). That is, areas of SI representing a specific part of the body are connected to those areas in SII that respond to the stimulation of the same body areas. Note also that both forward and backward reciprocal connections have been documented between SI and SII (e.g., Manzoni, et al., 1986).

Studies in humans using non-invasive (neuroimaging) techniques have confirmed the bilateral projection of the representation of the body to SII (e.g., Simoes, Alary, Forss, & Hari, 2002), and that the somatotopy is less fine-grained than in SI. That is, it has been shown that: (A) SII neurons with bilateral RFs (e.g., Iwamura, Iriki, & Tanaka, 1994) will respond to stimuli presented on both sides of the body; and (B) A somatotopic map (such as the somatosensory homunculus in SI) is also present in SII, but the point-to-point correspondence between body-parts and neural areas, where they are represented, is not as precise and straightforward as in SI. For example, while the direct stimulation of SI (in patients undergoing surgery to treat epilepsy) leads to a sensation that seemingly arises from the hand, a stimulation of adjacent SII leads to a sensation that extends outside the hand area (Mazzola, Isnard, & Mauguière, 2006). In fact, to a large extent, the somatotopic organization of SII seems to result from the precise, somatotopically-organized projections from SI, rather than from direct thalamic input (such as documented for SI; e.g., Friedman & Murray, 1986; Manzoni et al., 1986).

Much of the existing animal literature suggests that in the initial stages of somatosensory information processing, tactile stimuli that are delivered to one side of the body are first transmitted to the SI and SII cortices contralaterally via thalamocortical connections. After some intrahemispheric integration, the information is then relayed to ipsilateral SI and SII cortices via corticocallosal connections from SI to SI and SII, and from ipsilateral SII to contralateral SII for early interhemispheric integration. Several magnetoencephalographic (MEG) studies have reported the reliable activation of contralateral SI and bilateral SII in response to unilateral sensory stimuli (Del Gratta et al., 2002; Hari et al., 1993; Lin & Forss, 2002; Mima et al., 1998; Wegner et al., 2000) and ipsilateral SI activation has occasionally been observed (e.g., Nevalainen et al., 2006; Tan et al., 2004).

A number of animal and human studies have investigated (by means of histological sectioning) the somatosensory processing pathways in the brain, illustrating the possible flow of information from early sensory to motor areas (e.g., Friedman, Murray, O'Neill, & Mishkin, 1986). These studies have highlighted the existence of 62 pathways linking 13 cortical areas in the somatosensory/motor system. This compares to the 187 pathways linking 32 cortical areas for vision reported by Felleman and van Essen (1991). Strong connectivity has been demonstrated between areas 3a, 3b, 1, and 2 of SI. At higher levels of information processing, in addition to the already mentioned connections between SI and SII, direct and indirect links have also been documented between both of these areas and Brodmann's areas 5, 6, and 7, the supplementary motor area, the primary motor area, and the granular and dysgranular insula (e.g., Felleman & van Essen, 1991).

Animal studies have also investigated whether or not the flow of somatosensory information from early somatosensory areas to higher order processing areas in the brain occurs in a serial or rather in a parallel and distributed manner. A number of studies have shown that the complexity of the RF characteristics increases from area 3b to areas 1, 2, and 5 (e.g., Hyvarinen & Poranen, 1978; Iwamura et al., 1980, 1983, 1994). It is assumed that this increase in complexity results from the convergence of multiple inputs to single neurons via serial cortico-cortical connections. This organization would clearly suggest hierarchical/serial somatosensory processing in the post-central gyrus (e.g., Burton & Sinclair, 1996; see Iwamura, 1998, for a review). The serial organization of this brain area has also been confirmed by anatomical studies (e.g., Felleman & Van Essen, 1991; Künzle, 1978; Vogt & Pandya, 1978). Interestingly, this hierarchical form of information processing has also been reported, up to a certain extent, between SI and SII (e.g., Pons et al., 1987, 1992; though see Karhu & Tesche, 1999, for a study documenting the simultaneous early processing of somatosensory inputs in human SI and SII).

It is interesting to note that the hierarchical organization of connections between somatosensory brain areas seems, in certain respects, to mirror that found in the visual system. Indeed, the nine levels of the somatosensory and motor hierarchy proposed by Felleman and van Essen (1991) in the monkey brain are nearly as numerous as the 10 levels of the visual hierarchy, even though fewer than half the number of areas are involved. On the basis of this observation, one might wonder whether similarities in the neural organization of sensory areas might be suggestive of similarities at the level of cognitive information processing (and, therefore, if the mechanisms that have been proposed to give rise to visual consciousness are similar to those leading to the consciousness of tactile information).

On the basis of the research reviewed here, it has been shown that the initial connections supporting the processing of tactile information appear to be based on a serial/hierarchical architecture. Given this observation, one might expect that damage to the primary sensory processing areas should make both conscious and unconscious access to information impossible, even if higher order structures remain intact. By contrast, if consciousness arises at later levels of neural organization, damage to higher order areas should allow for the computation of that information, at least at an unconscious level of information processing (guaranteed by the sparing of early processing areas).

The Role of Early Somatosensory Areas in the Awareness of Tactile Information

In order to try to understand the role played by SI in the awareness of tactile information, one can look at the consequences of more or less temporary modifications of this structure for our awareness of information. It is now widely acknowledged that the somatosensory cortex is far from being a static neural structure (e.g., Nelles et al., 1999). Many different manipulations have proven effective in changing both the way in which the somatosensory cortex responds to external stimulation and the relative physical size of certain of its parts with respect to others. For example, a large body of evidence, from both animal and human studies, indicates that intense haptic/tactile training not only improves somatosensory perception, but also results in important changes in the cortical representations of the stimulated body part (e.g., Buonomano & Merzenich, 1998; Elbert, Pantev, Wienbruch, Rockstroh, & Taub, 1995; Jain, Qi, Collins, & Kaas, 2008; Pascual-Leone & Torres, 1993; Pons et al., 1991; Recanzone, Jenkins, Grajski, & Dinse, 1992; Saito, Okada, Honda,

Yonekura, & Sadato, 2007). Specifically, the relative size of a cortical representation seems to be positively correlated with the quality of performance on a particular task: The larger the representation, the better the performance. By contrast, certain forms of prolonged disuse, including immobilization or amputation of body parts, has been shown to lead to the shrinkage or disintegration of cortical representations/maps (e.g., Elbert & Rockstroh, 2004; Liepert, Tegenthoff, & Malin, 1995; Ragert et al., 2003). These studies appear to show that the consciously and explicitly reported aspects of a stimulus depend on changes occurring at the level of the somatosensory maps in SI.

Another means of investigating the role of the somatosensory cortex in the awareness of tactile information comes from studying lesions to this particular brain structure. It is rare, however, to find human patients with a brain lesion that selectively affects these brain areas (e.g., Brochier, Habib, & Brouchon, 1994). Consequently, most of the literature regarding the consequences of damage to this area comes from studies of selective ablation of specific brain tissue in monkeys. These studies have shown that ablation of the somatosensory cortex leads to the disruption of an animal's ability to respond to information regarding the texture (e.g., rough vs. smooth) of handled objects (e.g., Finger & Simons, 1976). Such results might be suggestive that damage to early sensory areas disrupts any possibility for the awareness of tactile information (regardless of the areas involved). Note, however, that animal studies do not allow one to dissociate between implicit and explicit levels of information processing, as can be done in humans (e.g., Faulkner & Foster, 2002).

One of the few recorded cases of brain damage confined only to the somatosensory cortex in humans was reported by Brouchon and colleagues (Brochier et al., 1994). They described a patient with a complete loss of somaesthetic sensitivity in his left arm resulting from damage to the primary somatosensory area in the right hemisphere. Interestingly, two months after his hospitalization, the patient was able to point correctly to stimulated locations on the affected limb even when blindfolded. Brochier et al. concluded that the accurate performance of the patient could have been mediated by the "covert" processing of somaesthetic information that unconsciously affected the sensorimotor control of hand movements. This unconscious form of sensory information processing, in the opinion of these researchers, was mediated by an alternative neural pathway.

Brochier et al. (1994) hypothesized that in addition to the system that projects tactile input from the dorsal column-lemniscal system via the ventro-postero-lateral nucleus of the thalamus (see the second section of this review), tactile information processing also involves a separate projection from the lateral posterior nucleus to the posterior parietal cortex (areas 5 and 7). This channel was thought to bypass primary somatosensory cortex and to be spared in the patient that they studied. They also thought that information provided by this channel was sufficient for controlling the coordinated movement of the deafferented hand. The presence of such a channel has been confirmed by Martin (1985), who showed that a portion of the medial lemniscal fibers project to the posterior nuclear group of the thalamus, and from here reach directly the posterior parietal cortices.

An alternative explanation for the performance of the patient studied by Brochier et al. (1994) has been suggested by Jeannerod et al. (1984), who had tested the same patient a few years earlier. They suggested that the sparing of somaesthetic afferents, which project directly from the VPL thalamic nuclei to the motor cortex in the patient, might have provided the ability to localize (by means of a correct

movement) stimuli on the affected limb, but not the possibility of detecting their presence explicitly. Both interpretations suggest that no residual awareness of information regarding the presence of tactile stimuli is available following damage to the somatosensory cortex. Thus the somatosensory cortex seems to be necessary for the awareness of touch. Before drawing any firm conclusions on the basis of Brochier et al.'s results, however, one should note that the study is based on the observation of a single patient (just as in another case study reported by Rode, Rossetti, & Boisson, 1995). The role of the somatosensory cortex in implicit and explicit information processing should, therefore, be addressed by further neuropsychological studies (as well as by neuroimaging studies).

One might wonder if a further, less studied, pathway could be responsible for certain aspects of implicit tactile perception. C tactile (CT) afferents offer one such possibility. In addition to the well-known system of fast-conducting myelinated (A-beta) afferents, the human hairy skin is innervated with a system of slowly conducting, unmyelinated (C), low-threshold, mechanoreceptive afferents (Vallbo et al., 1999). A patient, suffering from a loss of myelinated afferents, has been reported, who could still report the presence of tactile stimulation appropriate to activate the CT afferents (i.e., by means of the gentle stroking of the skin). fMRI of the brain areas activated in this patient during the presentation of tactile stimuli revealed, interestingly, the involvement of the insular cortex, but not SI and SII (Olausson et al., 2008; for evidence showing that the unmyelinated tactile afferents project to the insular cortex, see Olausson et al., 2002). Therefore, perhaps we should consider the possibility that at least certain aspects of our awareness of tactile information (e.g., those related to pleasant touch; see Gallace & Spence, 2010), might be mediated by the projections of the CT afferents to the insula. This would also suggest that the neural substrate of pleasant and discriminative touch might be, at least in part, different. This hypothesis should be confirmed by the collection of further experimental evidence.

A final line of evidence suggesting the importance of the somatosensory cortex for an awareness of information comes from studies of patients suffering from deafferentation (loss of afferent somatosensory projections due, for example, to amputation of a limb; e.g., Elbert & Rockstroh, 2004). Research has shown that tactile sensations may be evoked in the amputated portion of a limb by means of the appropriate stimulation (see James, 1887; Jensen, Krebs, Nielsen, & Rasmussen, 1983, 1984; Ramachandran & Hirstein, 1998; Weinstein, 1969; see also the novel *Moby Dick* by H. Melville; Perez-Barrero, Lafuente, & Marques, 2002). For example, it has been shown that the tactile stimulation of the stump of an amputated limb may elicit tactile, caloric, and/or pain sensations in the amputated phantom limb (e.g., Aglioti, Bonazzi, & Cortese, 1994; Aglioti, Cortese, & Franchini, 1994; Ramachandran & Hirstein, 1998; Weinstein, 1969; see Ramachandran, 1993, for a review).

It has been suggested that the phantom sensations in deafferented patients may reflect the consequence of the reorganization of the somatosensory cortex following the loss of input from the amputated limb (e.g., Berlucchi & Aglioti, 1997; Ramachandran et al., 1992). For example, phantom hand sensations, following stimulation of the face, might be caused by the appropriation of the initial representation of the amputated hand by the afferent input normally directed to the representation of the face (e.g., Pons et al., 1991; see Figure 1, showing that the

cortical regions of the somatosensory cortex that are thought to sustain the representation of the hands and face lie adjacent to one another).

The study of deafferented patients seems to show that the reorganization of the somatosensory cortex is likely responsible for the perception of tactile stimuli on regions of the body that are no longer connected with the relevant brain areas. That is, the presence of an intact representation of a limb in the somatosensory cortex guarantees the attribution of the neural signal reaching that area to that limb, even when it is physically absent. In other words, the awareness of tactile stimulation and its localization cannot be separated from the somatotopic organization of SI. In spite of this observation, however, it remains unclear whether tactile consciousness is based on a somatotopic or a spatial frame of reference. Indeed, it has been suggested that tactile sensations can be referred to positions on the body in external space, rather than on the skin surface, where the tactile receptors are actually located (e.g., Kitazawa, 2002; Wieland, 1960; Yamamoto & Kitazawa, 2001).

Towards a Model

Multisensory Modulation of Somatosensory Cortex Activity and Awareness of Information

Many studies have shown that the awareness of certain aspects of tactile stimulation (such as its intensity) can be modulated by the presentation of visual information (e.g., Azañón & Soto-Faraco, 2007; Hartcher-O'Brien, Gallace, Krings, Koppen, & Spence, 2008; Moseley, Parsons, & Spence, 2008; Serino, Farnè, Rinaldesi, Haggard, & Làdavas, 2007; Soto-Faraco & Deco, 2009; Taylor-Clarke, Kennett, & Haggard, 2002, 2004; Zhou & Fuster, 1997, 2000). For example, both tactile two-point discrimination thresholds and absolute detection thresholds are lowered when people are allowed to watch their body being touched (e.g., Schaefer et al., 2005; see also Tipper et al., 1998, for the report of improved reaction times to an invisible tactile stimulus when subjects were able to view the body part on a monitor). Similarly, the spatial tactile acuity of participants has been shown to improve when they look at their limb through a magnifying lens (e.g., Kennett, Taylor-Clarke, & Haggard, 2001; Schaefer, Heinze, & Rotte, 2008; see also Moseley et al., 2008; Ramachandran & Rogers-Ramachandran, 2008; Taylor-Clarke, Jacobsen, & Haggard, 2004).

Along similar lines, it has been suggested that the vision of prosthetic limbs can affect the processing of tactile information from the real limbs. Pavani, Spence, and Driver (2000) asked a group of participants to detect the position of vibrotactile stimuli while their upper limbs were placed out of view below an occluding screen. A pair of stuffed rubber washing-up gloves were placed in front of the participants in a position that was anatomically-compatible with that of their real limbs. Pavani et al. found that the participants often reported that the tactile stimuli arose from the location where they saw the rubber hands being stimulated rather than from its physical location (although on average, the participants' reports, measured by means of questionnaires, did not show "visual capture" of tactile sensations by the rubber hand). Sometimes, they even reported the sensation that the rubber hands were actually their real hands (see also Botvinick & Cohen, 1998; Durgin, Evans, Dunphy,

Klostermann, & Simmons, 2007; Ehrsson, Spence, & Passingham, 2004; Tastevin, 1937; Tsakiris & Haggard, 2005).

Interestingly, the latest research by Moseley et al. (2008) has shown that as the unseen limb is “replaced” by an artificial counterpart, it becomes slightly, but significantly, cooler, and the explicit identification of tactile information presented from this area of the body is slowed down. Both thermoregulation and the amount of time required by tactile information to gain access to awareness seem to be similarly affected when a certain part of the body is visually replaced by another “artificial limb”. In other words, it seems that whenever the sense of body ownership is manipulated, there are important consequences for the neural systems responsible for supporting the awareness of touch and even for those responsible for the maintenance of the homeostatic control of the body.

It has been suggested that visual manipulations of tactile awareness, such as those reviewed in this section, might act at the level of somatosensory cortex (e.g., Schaefer, Heinze, & Rotte, 2005; Taylor-Clarke et al., 2002; Zhou & Fuster, 1997, 2000). Possible confirmation of this claim comes from a study by Schaefer, Flor, Heinze, and Rotte (2006), in which participants were asked to look at a video of a hand being touched on the first digit. In one experimental condition, the real hand of a participant (hidden from view) was touched in synchrony with the touches seen on the video, while in another condition the visual and physical touches were presented asynchronously. Using magnetoencephalography (MEG), the authors found that the cortical representation of the participant’s first finger moved to a more inferior location (a phenomenon related to improved tactile acuity; e.g., Pleger et al., 2001) during synchronous, as compared to asynchronous, stimulation or rest. Even more relevant, is the observation that this modulation of the SI map was positively correlated with the feeling that the touch seen in the video represented the touch on the participant’s real hand.

In the section on the neural organization of the somatosensory cortex, it was shown that this part of the brain has dense connections with premotor and posterior parietal areas (as well as primary motor areas). It is relevant to point out that in these neural structures bimodal neurons were found that respond to both tactile and visual stimuli (e.g., Graziano & Gross, 1995; Graziano, Hu, & Gross, 1997; see Graziano, Gross, Taylor, & Moore, 2004, for a review). It is, therefore, possible that activation from these areas alters processing in SI via back-projections. It is worth noting that animal studies have observed these forms of top-down projection from multisensory to unisensory areas for the visual modality (e.g., Rockland & Ojima, 2003; see also Driver & Spence, 2000, for discussion of this point). As far as the tactile modality is concerned, animal studies in monkeys have shown that certain neurons in SI respond to visual stimuli that have previously been associated with touch (Zhou & Fuster, 1997; see also Iriki et al., 1996). Moreover, it has also been shown that some of these neurons respond over a period of time (that is, they keep firing after the disappearance of the stimulus that elicited the response in the first place). This result has been taken to suggest the presence of a sort of cross-modal temporary memory located in SI (Zhou & Fuster, 2000; see Gallace & Spence, 2009, for a recent review of the cognitive and neural mechanisms that underpin tactile memory).

The presence of short term forms of memory is a crucial factor for giving rise to an awareness of sensory information, a concept that has often been described by Edelman’s (1989) expression “the remembered present” (used to define the very short

period of time where we are aware of something; see Gallace & Spence, 2009 cf. Wolfe, 1999). This observation clearly highlights the importance of brief forms of memories across the somatosensory cortex for our awareness of touch. The presence of time-delayed responses to visual and tactile information in SI has given rise to two possible interpretations (see Zhou & Fuster, 1997): (A) The phenomenon is determined by the plasticity of the somatosensory cortex. That is, because of the prolonged training and temporal association between visual and tactile stimuli, somatosensory neurons learn to respond to the visual stimuli that are associated with the tactile stimuli; (B) during the execution of the task, those cells are activated by feedback from the posterior parietal cortex, where the visual information is processed. These observations highlight the importance of both the somatosensory cortex and its plasticity for giving rise to an awareness of tactile stimuli. At the same time, however, they also suggest that the connectivity between this area of the brain and multisensory neural structures plays a crucial role in giving rise to awareness of information (see Gallace & Spence, 2008).

Interestingly, it is not only visual stimulation that has been found to affect tactile information processing and the awareness of information by means of the modulation of activity at the level of the somatosensory cortex. Studies of sensory suppression have shown that self-generated movement increases the detection threshold for tactile stimuli presented on a moving body part (Juravle, Deubel, Tan, & Spence, 2010) and, to a smaller extent, on more remote sites of the body surface (e.g., Williams, Shenasa, & Chapman, 1998). The ability of participants to explicitly report the presence of tactile stimuli decreases as a function of the distance between the moved body part and the position where the tactile target stimulus is presented (e.g., Williams et al., 1998). That is, the closer a target stimulus is to the part of the body that is moved, the more likely it is that participants will fail to detect the stimulus. This result can be taken to suggest a modulation of activity across SI by means of efference copy signals from premotor brain areas (e.g., Christensen et al., 2007; cf. Gallace, Zeeden, Röder, & Spence, 2010).

Sensory suppression in animals (rats) has also been shown to be caused by an increase in the overall level of arousal. This phenomenon has been found to be determined by the activity-dependent depression of thalamocortical synapses (Castro-Alamancos & Oldford, 2002). That is, activity in subcortical brain areas can also affect an organism's awareness of information by acting upon the primary somatosensory cortex.

The results of the sensory suppression studies reported above, just as for those studies related to the modulation of tactile processing by means of visual information, stress that the activity of different brain areas (and, in particular, those involved in movement planning and spatial information processing; see Gallace & Spence, 2008; cf. Gallace et al., 2010) can modulate the activity of somatosensory cortex, and thus our awareness of tactile information.

When Touch is only in the Mind of the Beholder: A Role for the Somatosensory Cortex in "Illusions" of Touch?

The awareness of incoming tactile information does not necessarily arise from stimuli that are delivered physically. The visual literature has shown that percepts can be reported consciously, at least under certain conditions, even when their physical counterpart is absent. Illusions, hallucinations, and synaesthetic perceptions (as well as dreams, but critically not mental imagery) all fall into this category. Given that the

activation of early sensory areas has been shown to play a role in at least some of these phenomena (e.g., Bressloff, Cowan, Golubitsky, Thomas, & Wiener, 2001), we discuss this topic as far as it concerns the tactile modality, *synaesthetic touch*. Tactile sensations can be elicited, in certain individuals, by the presentation of non-tactile stimuli. This is the case for certain individuals with a condition known as synaesthesia. In fact, in people affected by synaesthesia, stimulation in one sensory modality results in the simultaneous subjective experience of sensation in another sensory modality (e.g., Baron-Cohen & Harrison, 1996; Cytowic, 2002; Cytowic & Eagleman, 2009). As far as the tactile modality is concerned, Blakemore, Bristow, Bird, Frith, and Ward (2005) described the case of a woman for whom the observation of another person being touched was experienced as tactile stimulation on the equivalent part of her own body (thus supporting the existence of a visuotactile form of synaesthesia; e.g., Banissy & Ward, 2007; see also Cytowic, 1993, 2002, for the description of a tactile-gustatory form of synaesthesia). Interestingly, Blakemore and her colleagues (2005) also measured the brain activity (by means of fMRI) of their patient, together with a group of non-synaesthetic individuals, during the observation of touch to different parts of another body or of an object. They found that the somatosensory cortex, the premotor, and parietal cortices were activated both in the non-synaesthetic participants and in the synaesthetic patient by the mere observation of touch. No actual tactile experiences, however, were reported by non-synaesthetic participants. This activation was somatotopically organized, such that observation of touch to the face activated the area of SI corresponding to the head, whereas observation of the neck being touched did not (compared to the activation found when the participant's body was touched). Note, however, that in the patient, the level of SI activation was higher than in the control group and also included the anterior insula (the insular cortex has been shown to be involved in the storage of tactile experiences; see Gallace & Spence, 2008, for a review).

Blakemore et al.'s (2005) results highlight the fact that SI is involved in the awareness of touch even under conditions in which tactile information is not actually presented (as in the case of certain synaesthetes; though see Day, 2005). It also seems that the intensity of activation (in SI and in the neural circuit activated by the observation of touch) can account for the difference in tactile experience reported by the synaesthetic patient and non-synaesthetic participants. That is, activation in these brain areas might need to reach a certain threshold in order to elicit an awareness of tactile stimuli. Blakemore and colleagues' results also strengthen the claim that synaesthesia-like sensations (although qualitatively and quantitatively different from those experienced by synaesthetes; e.g., Cytowic, 1993) can also be elicited in non-synaesthetic individuals under specific stimulation conditions (e.g., Durgin et al., 2007; Gallace & Spence, 2005).

Blakemore and her colleagues (2005) interpreted their finding in terms of the presence in their patient of an abnormally-high activation of the *tactile mirror system*: A system that responds in a similar manner to touch when seen in other individuals as is reported for neural systems that respond to the observation of an action performed by an external agent (e.g., Keyser et al., 2004; Rizzolatti, Fogassi, & Gallese, 2001). Note, however, that a study by Keyser et al. (2004) revealed that the activation of the tactile mirror system did not involve activity in SI but only in SII (although a non-significant trend towards SI activation was also reported). We believe that the involvement of SI, and also the temporal dynamic of activation among the different brain areas involved in visual-touch synaesthetic experiences, should be investigated

further. Moreover, research should also investigate the involvement of the brain areas responsible for the storage of tactile information, such as the postero-ventral insula, on the activation of the somatosensory cortex.

Tactile hallucinations. It is not surprising to find that very little research has been conducted on the topic of tactile hallucinations or delusions, as compared to the much larger body of research dedicated to visual hallucinations (e.g., Bressloff, Cowan, Golubitsky, Thomas, & Wiener, 2001; Kluver, 1966). Reported cases of tactile hallucinations vary from more basic tactile sensations such as imaginary itches (Darwin, 1796), formication (i.e., the abnormal sensation as of insects crawling in or upon the skin; cf. Caporael, 1976; Matossian, 1982), pinching, rubbing (Regis, 1906), and having the skin covered in fur (Storring, 1907), to far more complex perceptual experiences, such as being kissed, having someone lying by one's side, and more or less bizarre sexual experiences (Kraepelin, 1919; see Berrios, 1982, for a review; see also Grimby, 1993 for the report of tactile hallucinations in elderly people following bereavement in 6% of cases). In a number of different cases, tactile hallucinations have been associated with an organic state such as brain injury, dementia, hypophyseal tumor, and diabetes, rather than a non-organic psychosis (Skott, 1978). For example, in a sample of 46 patients affected by tactile hallucinations (namely delusions of infestation), Skott found that about 50% exhibited clinical signs of an organic brain syndrome, 61% had pathological electro-encephalogram (EEGs), and 12% had malignant disease (i.e., carcinoma).

A case of tactile (as well as visual) hallucinatory sensations following brain damage has been reported by Halligan, Marshall, and Ramachandran (1994) in a patient following right hemisphere stroke. The patient exhibited a number of hallucinations (compatible with a diagnosis of Charles Bonnet Syndrome; e.g., Morsier, 1936; Schultz & Melzack, 1991), together with a moderate left-sided neglect and left visual field deficits, in the first few days after hospitalization. These symptoms progressively receded and then completely disappeared approximately a year after the first observation. The hallucinations were primarily visual and regarded human figures, animals, and aerial views. On different occasions, the patient also reported tactile sensations related to the object of her hallucinations. For example, she not only experienced the presence of a dog (actually one of her dogs that had died many years earlier), but also reported the sensation that the dog's fur was wet to touch, the same as when he had come back to her following a walk in the rain (p. 466). She also reported the tactile feeling associated with poking her husband's arm in order to wake him up (p. 466).

The patient's lesion had affected the right temporal pole, caudate nucleus, lower basal ganglia, insular cortex, putamen, and posterior frontal cortex. On the basis of a series of considerations, Halligan and his colleagues ruled out the possibility that the patient's hallucinations were due to a psychotic state or to a lack of central control. By contrast, they suggested that they were likely determined by the brain damage suffered by the patient and, in particular, by a form of sensory deprivation due to a disconnection between higher-order and sensory brain areas. Note, however, that this interpretation was only based on the visual hallucinations reported by the patient. In fact, Halligan and his colleagues do not comment on the possible cognitive and neural mechanisms of tactile hallucinations reported by their patient. If visual hallucinations are produced when visual association areas, deprived of their normal input (due to lesions of the connections between higher visual areas such as V4 and

sensory visual areas such as area 17), fire spontaneously, one might wonder if a similar mechanism could also cause the tactile hallucinations reported here. We believe, however, that there is another potential interpretation.

Neuroimaging studies have shown that both the posteroventral insula (a structure that was also damaged in the patient studied by Halligan and his colleagues) and perirhinal cortex are involved in the storage of tactile information regarding haptically explored stimuli (e.g., Bonda, Petrides, & Evans, 1996; see Gallace & Spence, 2009, for a review). It can be speculated that tactile (as well as visual) hallucinations might be caused by the faulty activation of those brain areas responsible for tactile memories. Eventually, a misfiring of the circuit that sustains tactile memories (and that includes the somatosensory cortex as well as areas responsible for the active exploration of the stimuli; see Gallace & Spence, 2009) could, at least in part, explain the hallucinatory tactile phenomena reported by Halligan and his colleagues. Alternatively, however, the tactile component of the hallucinations seen in this patient might simply result from the effect of higher order visual areas upon those responsible for the processing and/or storage of tactile information. In fact, it has been shown that tactile sensations can be elicited, under certain conditions, by visual stimulation (e.g., Durgin et al., 2007; see also previous section).

Since the advent of neuroimaging, a few studies have attempted to investigate the involvement of different brain structures in tactile hallucinations. In particular, the majority of efforts have been directed at analyzing a form of visuo-tactile delusion known as *delusional parasitosis* (e.g., Huber, Karner, Kirchler, Lepping, & Freudenmann, 2008; Musalek et al., 1989; see de Leon, Antelo, & Simpson, 1992, for an early review). Delusional parasitosis is a syndrome characterized by the conviction (accompanied by reports of tactile and sometimes visual sensations) that small creatures are infesting one's skin. In one of the first attempts to determine the neural correlates of this condition, Musalek and colleagues (1989) studied 10 unmedicated patients who reported delusions of parasitosis using single photon emission computed tomography (SPECT) to measure regional cerebral flow. They found a relative reduction of regional cerebral flow in the inferior temporal regions. Following this early study, the majority of the reports accumulated over the years suggest that delusions of parasitosis commonly occur after damage to subcortical or cortical brain regions, often in the temporo-parietal region of the right hemisphere (e.g., Adunsky, 1997; Blanke, 2008; Blasco-Fontecilla et al., 2005; De Leon et al., 1997; Flynn et al., 1989; Maeda et al., 1998; Nagaratnam & O' Neile, 2000; Narumoto et al., 2006; Safer et al., 1997; Takahashi et al., 2003).

In a recent study, Huber et al. (2008) used MRI in order to determine whether structural lesions of brain regions could be found in patients with delusions of parasitosis. On the basis of their findings, they suggested that structural lesions in the striatum, predominantly the putamen, might account for this syndrome at least in those patients with a medical condition (but not in those with pre-existing psychiatric illness). Even more relevant to the topic of the present review is the observation by the authors that the putamen contains bimodal cells with visual and tactile receptive fields, which help to encode the location of stimuli mainly near the face (e.g., Graziano & Gross, 1994; Gross & Graziano, 1995). On the basis of these considerations, they claimed that the itching and tactile hallucinations, as well as

somatic delusions seen in patients, are mediated through a striato–thalamo–parietal network.

It is important to note that a recent neuroimaging study in humans has shown (by means of diffusion tensor imaging -DTI- tractography) that the putamen is interconnected with the prefrontal cortex, primary motor area, primary somatosensory cortex, supplementary motor area, premotor area, cerebellum and thalamus (Leh, Ptito, Chakravarty, & Strafella, 2007). Based on this observation, we believe that the primary somatosensory cortex may well be involved in hallucinations such as those reported in delusions of parasitosis. One might wonder, however, whether the role of this structure in eliciting the phenomenon is determined by subcortical to cortical (by means the direct connections of SI with the putamen) or cortical to cortical activation (mediated by the involvement of areas of the frontal and/or parietal cortex). These two explanations are not necessarily mutually exclusive.

The cutaneous rabbit illusion. The cutaneous rabbit is a well-known somatosensory illusion, in which repetitive and rapid sequences of stimulation (each composed of about five consecutive vibrations) at two or more skin locations can, under certain conditions, lead to illusions that the space between the actual stimulation on the body sites was also stimulated although no physical stimulus was delivered at that location (e.g., Blankenburg, Ruff, Deichmann, Rees, & Driver, 2006; Geldard & Sherrick, 1972; Goldreich, 2007; Kilgard & Merzenich, 1995). Under such conditions, participants report the perception of a continuous sequence of stimuli moving across the skin (as if a rabbit hopped along successive locations).

A number of early behavioral studies have shown that tactile “saltation” does not occur when the stimuli are presented to non-adjacent regions of the skin (i.e., from the hand to the foot; e.g., Geldard & Sherrick, 1983). This empirical observation has been taken to suggest that the cutaneous rabbit illusion might be constrained by the anatomical organization of the somatosensory system (e.g., Geldard, 1982; Geldard & Sherrick, 1983). That is, the illusory perception of additional tactile stimuli in the sequence might arise at very early stages of information processing (e.g., in the somatosensory cortex; e.g., Cholewiak, 1999; Geldard, 1982).

Eimer et al. (2005), however, recently reported that tactile saltation can also be observed under conditions in which some of the stimuli are presented to each arm (i.e., to non-contiguous regions of the somatosensory cortex). On the basis of these results, Eimer and his colleagues concluded that the cutaneous rabbit illusion does not necessarily arise at an especially early stage of information processing. They proposed, instead, that the phenomenon is likely to arise in higher order brain areas, such as the secondary and posterior parietal somatosensory areas, where there are a large number of neurons with bilateral RFs (e.g., Iwamura et al., 1994).

The neural mechanisms underlying the cutaneous rabbit illusion have recently been directly investigated by means of neuroimaging techniques. Specifically, in a study by Blankenburg and colleagues (2006), the brain activity of participants during the perception of the illusion across the arm (leading to the perception of an intervening location being stimulated) was measured and compared to a control condition of veridical stimulation at the same skin sites. The results demonstrated that illusory sequences activated contralateral primary somatosensory cortex at a somatotopic location corresponding to the filled-in illusory perception on the forearm. Interestingly, the amplitude of this somatosensory activation was comparable to that

for veridical stimulation including the intervening position on the arm. The illusory percept additionally activated areas of premotor and prefrontal cortex.

Blankenburg et al.'s (2006) results provide evidence that illusory somatosensory percepts can affect brain activity, within the primary somatosensory cortex, in a manner that correspond somatotopically to the illusory percept reported by participants. The results of this study, however, don't argue against the possibility that SI activity could be driven in a top-down manner by the activation of higher-order processing areas (e.g., premotor and prefrontal cortex), just as Eimer et al.'s (2005) study seemed to suggest. It would be interesting in future research to use a synergy between those brain imaging methodologies that allow for more accurate temporal resolution (such as EEG) and those that allows for higher spatial resolution (such as fMRI; e.g., Dale et al., 2000). This would help to understand the temporal sequence of activation of different areas of the brain in eliciting such an illusory percept.

The funneling effect and supernumerary limbs. The tactile funneling illusion refers to the illusory perception of a tactile stimulus at a single unstimulated skin site, situated between a pair of stimulated locations on the skin. Inputs at lateral sites are "funneled" in a central position with respect to the two stimulated areas (e.g., Gardner & Spencer, 1972; von Békésy, 1967). A recent study by Chen, Friedman, and Roe (2008) investigated the brain correlates of the funneling effect in monkeys by means of intrinsic-signal optical imaging. Their results showed that the simultaneous stimulation of two fingertips produced a single focal cortical activation between the single fingertip activation regions in primary somatosensory cortex area 3b (see also Gardner & Spencer, 1972). Interestingly, even though no physical stimulus occurred at the funneled site, the cortical response obtained via the illusory effect was comparable in size to that of an actual single-digit stimulus.

Although Chen et al.'s (2008) study highlights the fact that the illusory perception of a tactile stimulus activates SI, it does not shed any light regarding the involvement of further brain sites in eliciting the effect. On the basis of this study, we do not know whether the activation of SI is sufficient or necessary to evoke awareness of the illusory tactile percept. Further studies, where cortical activity is concurrently measured at different brain locations, will need to be performed in order to answer this important question. By contrast, what seems to emerge from published studies of tactile illusions, such as the cutaneous rabbit or the funneling effect, is that topographic representation in SI reflects the perceptual, rather than the physical, location of peripheral stimulation that we become aware of. That is, the awareness of tactile information is related to activation of SI, rather than necessarily to the actual involvement of the tactile receptors stimulated at the body surface. Recent confirmation of this claim has come from a study that investigated the effect of supernumerary limbs on the activation of SI (Schaefer, Heinze, & Rotte, 2009).

Schaefer et al. (2008) used an artificial hand and arm that appeared visually to be connected to the participants' own body to give the impression that they had a supernumerary third arm (in a central location between the real hands; see also Halligan, Marshall, & Wade, 1993, for the report of a patient affected by the delusional perception of a supernumerary phantom limb after damage to the right basal ganglia; and Hari et al., 1998, for the case of a patient who reported the presence of a third hand, and less frequently leg, after lesion to the right frontal lobe and corpus callosum). The behavioral data (obtained by means of a questionnaire) showed that

six out of eight participants tested felt as if they had three arms! Even more interesting is the fact that the activation of SI, measured by MEG, was modulated by the perceived presence of the supernumerary limb (i.e., the cortical representation of the thumb shifted to a more medial and superior position). This modulation was found to be predictive of the strength of the feeling that the third arm actually belonged to the participant. This phenomenon certainly bears comparison with that of phantom sensations in amputated limbs, where deafferented patients report tactile sensations arising from a “non-existent” limb (see the previous section). For both phenomena, consciousness of touch is reported from a location that does not physically belong to the body, and both phenomena seem to depend, at least in part, on neural activity occurring in SI (e.g., Schaefer et al., 2008a). This observation also helps to emphasize the important role that body ownership exerts on our awareness of tactile sensations.

The results of the studies on tactile illusions, together with those on supernumerary limbs, open up the intriguing possibility that the awareness of tactile stimulation can somehow be “rebuilt” or “re-wired” (by means of neural prosthesis; see Abbott, 2006; Velliste, Perel, Spalding, Whitford, & Schwartz, 2008) in patients who have suffered from deafferentation (or even totally created in participants exposed to additional virtual or artificial limbs; see Schaefer et al., 2008) by directly acting upon SI.

Taken together, the results highlighted in this section illustrate the fact that an awareness of tactile information can arise regardless of the presence of actual stimulation on the skin surface. They also show that this effect relies, at least in part, on the somatotopic representation of the body found in SI.

Beyond the Primary Somatosensory Cortex

In the previous sections, we have seen that the results of a number of studies point toward areas outside the somatosensory cortex as having an important role in the awareness of tactile information. In this section, we review those studies that have directly investigated whether or not activation across the somatosensory cortex is sufficient to elicit an awareness of touch. Lafuente and Romo (2005) investigated the role of the somatosensory cortex in eliciting an awareness of tactile stimuli in monkeys by means of direct intracellular recording (with an array of seven independent movable microelectrodes). They reported a lack of covariation between monkeys’ perceptual reports of near-threshold tactile stimuli delivered to the fingertips, and the response of neurons in the primary somatosensory cortex. By contrast, the activation of SI was found to be proportional to the intensity of the stimuli presented. That is, SI seems not to be responsible for the monkey’s awareness of tactile stimulation. One of the first attempts to investigate the involvement of the human somatosensory cortex in the awareness of tactile information was made by Libet, Alberts, Wright, and Feinstein (1967). They recorded the averaged evoked response to tactile stimulation subdurally from the somatosensory cortex (in patients undergoing brain neurosurgery for various clinical conditions). They found a response in this area even when the intensity of the stimulus presented was set below the perceptual threshold. That is, the signal elicited by the stimulus was processed in this area regardless of the participant’s awareness of it. By contrast, however, Libet and his colleagues also found that late components (up to and exceeding 500 ms) that followed the primary evoked potential were correlated with sensory awareness and were thus deemed necessary for the stimulus to be consciously perceived. On the basis

of their findings, Libet et al. concluded that the primary evoked potential in SI does not constitute a sufficient condition for the perceptual awareness of tactile sensations.

More recently, an MEG study by Preissl et al. (2001) investigated tactile consciousness in two patients scheduled for neurosurgery to remove a brain tumor, who reported a lack of somatosensory sensations. Magnetic imaging revealed early neural activations in the primary somatosensory cortex in both patients (within an interval of 40 ms from stimulus onset), but the absence of any later activation (in the 60 and 150 ms components of the MEG signal) in either the primary or associative areas (parietal cortex, BAs 5, 7, and 40). On the basis of these results, Preissl et al. concluded, as had Libet et al. (1967), that parietal areas posterior to SI are necessary for the conscious processing of somatosensory stimuli (see also Ray et al., 1999; see de Lafuente & Romo, 2005, for similar results reported using single unit recordings in monkeys).

It is worth noting that Palva and colleagues (2005) also used MEG in order to investigate the correlation of neuronal oscillations with conscious perception of somatosensory stimuli presented at threshold intensity levels. They reported that broadband cortical activity in a network comprising the somatosensory, frontal, and parietal regions was phase-locked with the subsequently perceived stimuli as early as 30-70 ms (and up to 150 ms) from stimulus onset. By contrast, stimuli that went unnoticed did show a weak phase-locked activity that was confined to somatosensory regions.

Schubert et al. (2006) tested neurologically-normal participants in a study in which they presented suprathreshold tactile stimuli and recorded event-related potentials (ERPs) in response to stimuli that had been correctly detected and to stimuli that went undetected (following the presentation of backward masking). They found that the early ERP components (P60 and N80), generated in the somatosensory cortex contralateral to the stimulated region of the body, were uncorrelated with the perception of the stimulus. By contrast, the amplitude enhancement of the later ERP components (P100 and N140 in parietal and frontal areas, respectively) were only observed when target stimuli were consciously-perceived. Schubert et al. concluded that the early activation of SI is simply not sufficient to elicit conscious perception of a stimulus. By contrast, tactile consciousness could be mediated by the activation of frontal and parietal areas (see also Sarri et al., 2006; for the report of activation, as measured by fMRI, of the parietal cortex in addition to the somatosensory cortex when a patient, exhibiting extinction, became aware of contralesional tactile information, but not on trials in which he was unaware of such information).

Evidence against the primary somatosensory cortex playing a crucial role in the awareness of tactile information comes from studies of neurological patients affected by extinction. Patients with right posterior temporo-parietal cortical lesions often exhibit extinction to tactile double simultaneous stimuli (e.g., Driver & Vuilleumier, 2001; Marzi, Girelli, Natale, & Miniussi, 2001). For instance, when both hands are stimulated simultaneously, the patient fails to consciously detect and report the contralesional stimulus in the pair, although they can report contralesional and ipsilesional stimuli when presented in isolation (see Marcel et al., 2004). Healthy participants can also show a pre-morbid susceptibility to spatial migration and integration of tactile sensations that is in some sense similar to that found in patients, and this might be exaggerated by brain damage (Marcel et al., 2006).

In a recent study by Beversdorf, Hughes, and Heilman (2008), the volume of SI activation in a patient with contralesional extinction (due to a stroke that affected the temporal lobe) was measured using fMRI. The authors reported that even if the patient demonstrated extinction during behavioral testing, the activation of SI measured on both the contralesional and ipsilesional sides was within the range of activation observed in control participants. On the basis of these findings, Beversdorf and colleagues suggested that extinction in patients with a right temporal lobe stroke results from processing abnormalities that occur only after the afferent tactile stimuli are processed in SI. That is, higher order processing areas are likely responsible for the lack of awareness of tactile stimuli in these patients. Similar results were obtained by Kobayashi, Takeda, Kaminaga, Shimizu, and Iwata (2005) in a patient affected by extinction due to damage of the right parietal cortex. Kobayashi and his colleagues also concluded that activation of SI is insufficient to sustain the awareness of sensory stimuli.

Other studies of neurological patients who have been affected by extinction have further highlighted the involvement of areas above SI in the awareness of tactile information. In particular, Maravita (1997) reported the case of a brain-damaged patient affected by tactile extinction and neglect (the inability to consciously report the presence of stimuli presented in the contralesional side of the space and/or of their body; e.g., Driver & Vuilleumier, 2001; see also Vallar, 2001; Vallar, Rusconi, Bignamini, Geminiani, & Perani, 1994, for the neural correlates of neglect and extinction). This patient was unable to report any of the qualities of objects held in his contralesional hand when another object was simultaneously presented in his ipsilesional hand. Critically, however, when the patient was asked to compare the size of two spheres (one presented to each hand), his judgments were biased by the size of the sphere previously held in his contralesional hand, although he had been unable explicitly to report its presence versus absence (see Uznadze, 1966). In this patient, implicit tactile information processing was preserved, while the ability to explicitly report certain qualities of the haptically explored stimuli was impaired. Crucially, the patient studied by Maravita was affected by a right brain lesion that included the lingual and fusiform gyri, the retrosplenial area, the angular gyrus, and part of the superior parietal lobule, but not the primary somatosensory cortex.

The studies reviewed in this section clearly show that, by itself, the activation of early sensory areas is insufficient to sustain an awareness of tactile sensations. By contrast, other higher order structures, comprising both parietal and frontal areas, seem to be necessary for tactile consciousness. This result compares to those obtained in visual studies where it has been shown that the involvement of a number of neural structures above V1 is crucial for the awareness of visual information to emerge (e.g., Rees, 2007; Tong, 2003).

A Neurocognitive Model that can Explain Awareness of Touch

On the basis of the studies discussed in this review, we suggest a model for the awareness of tactile information. This model constitutes an updated and modified version of the model proposed by Gallace and Spence (2008). We believe that the neural circuits involved in the awareness of tactile information are the same as those that are involved in the processing and storage of that information (see Gallace & Spence, 2008; cf. Berti et al., 2005). Moreover, on the basis of the evidence reviewed here, we believe that information from SI does not directly enter awareness, but it is necessary in order for it to arise: No awareness of tactile information is possible

without SI. This claim is mainly supported by the data obtained from the study of neurological patients with brain damage confined to the somatosensory cortex (Brochier et al., 1994). On the other hand, activity in SI contributes to tactile awareness regardless of the actual physical presence of tactile stimulation (e.g., Blakemore et al., 1995; Blankenburg et al., 2006). The results of the studies on deafferented patients (see James, 1887; Jensen, Krebs, Nielsen, & Rasmussen, 1983, 1984; Ramachandran & Hirstein, 1998; Weinstein, 1969) and those on tactile illusions and hallucinations (e.g., Blankenburg et al., 2006; Leh et al., 2007; Schaefer et al. 2008) support the latter claim.

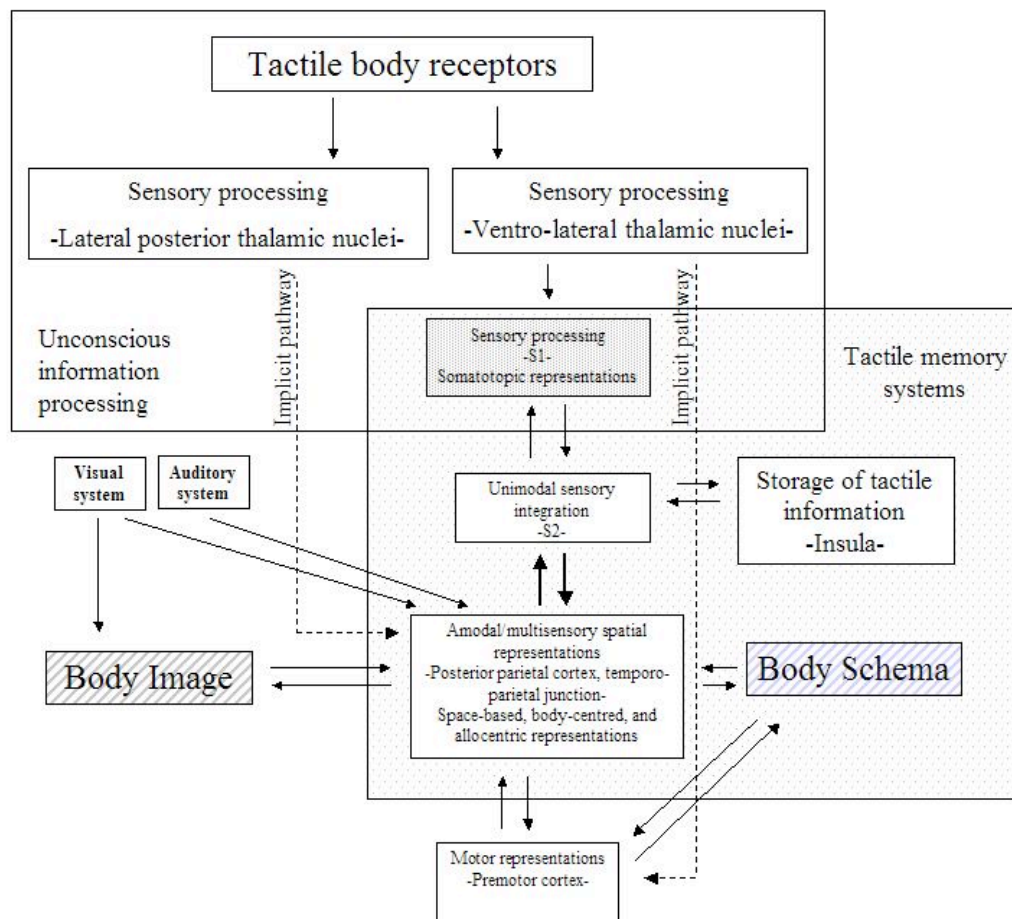


Figure 2. A putative neuro-cognitive model supporting the consciousness of tactile information in humans. See the main text for details.

The study of patients affected by spatial disorders, such as neglect and extinction (e.g., Beversdorf et al., 2008; Kobayashi et al., 2005; Maravita, 1997), and neuroimaging studies (e.g., Christensen et al., 2007) yield evidence consistent with the suggestion that an awareness of touch requires activation of a network comprising higher-order processing areas. In particular, activation of those areas responsible for the processing of the spatial aspects of the stimuli and those involved in planning movements is required (e.g., Gallace & Spence, 2008; Kitazawa, 2002; cf. Graziano, 2001; see Figure 2 for a representation of the model). As suggested by the study of

patients with damage to the somatosensory cortex (Brochier et al., 1994), tactile consciousness can also be modulated by the activity of thalamo-cortical circuits. According to our model, SI constitutes a matrix (cf. Melzack & Wall, 1965) upon which the consciousness of touch can form. We also suggest that its essential role is primarily linked to the fact that this area of the brain supports a plastic neural representation of the entire body surface.

Description of the model. Tactile information is transmitted from peripheral receptors distributed throughout the skin via the dorsal column-medial lemniscus pathway to the thalamic nuclei and from there to SI. In SI, information is represented on the basis of a somatotopic frame of reference (e.g., Penfield, 1950; Romo et al., 1998). As suggested by neurophysiological and neuropsychological data, this stage of information processing does not enter into consciousness (e.g., Palva et al., 2005; Preissl et al., 2001; Schubert et al., 2006; Schwartz et al., 2005; see also Lafuente & Romo, 2005). Activity in SI, however, generated and/or increased by feedback and feedforward connections between SI and higher order areas (e.g., Manzoni et al., 1986), is associated with the awareness of tactile stimuli. Note that the importance of feedback activity from higher order to early sensory areas has also been suggested to play an important role in certain aspects of visual awareness (e.g., Lamme et al., 2000; Pascual-Leone & Walsh, 2001).

At least two different neural pathways are responsible for the implicit processing of tactile stimuli (e.g., when SI is damaged). One connects the ventro-thalamic nuclei to premotor brain areas (cf. Jeannerod et al., 1984). The other pathway, confirmed by histological studies (e.g., Martin, 1985), connects the lateral posterior nucleus of the thalamus to the posterior parietal cortex (see Brochier et al., 1994). Both of these systems are also thought to generate responses to tactile stimuli when their conscious report is absent (e.g., Brochier et al., 1994; Jeannerod et al., 1984).

Information from SI is then transferred (in a “cascading” fashion between neurons with progressively-larger RFs) to SII, where tactile information is integrated (note that some SII neurons have bilateral RFs; e.g., Iwamura et al., 1994). SII is connected with other higher order areas of the parietal cortex, with the insula, and indirectly to the premotor cortex (note that connections between area 2 and the supplementary motor area have also been reported; see Felleman & Van Essen, 1991). Higher order parietal regions have multisensory/amodal properties and support representations based on different spatial coordinate systems (e.g., Graziano & Gross, 1995; Graziano et al., 2004). The characteristics of these areas allow information from different sensory modalities (i.e., vision and audition) to exert an effect on people’s awareness of tactile information (e.g., Hartcher-O’Brien et al., 2008; Serino et al., 2007; Zhou & Fuster, 1997, 2000; cf. Gallace & Spence, 2008). The awareness of touch results from the reciprocal interactions occurring between these structures. This system also supports the storage of tactile information.

We have included a further functional component into the system outlined in Figure 2: the body schema. Note that this component, just as the body image, is not anatomically separated from the rest of the model as the box in Figure 2 might suggest. Instead, the body schema arises from interactions taking place at different levels of the model. For example, evidence suggests that the insula (in particular the posterior part of it) plays an important role not only in the storage of tactile information, but also in supporting certain aspects of the body schema and body

image (e.g., Baier & Karnath 2008; Karnath, Baier, & Nagele, 2005; see also Vallar & Ronchi, 2009). Despite this observation, the link between this area of the brain and the body schema is not represented in our model.

We would like to stress that the neural system that supports the body schema interacts with the system that supports awareness of touch, rather than to highlight the anatomical superimposition and reciprocal connections of the brain areas responsible for these functions/representations. The presence of the body schema in the model indicates that tactile consciousness is somehow related to the modification of the body schema (e.g., Haggard & Wolpert, 2005; Paillard, 1999). The body schema, however, is not thought to enter awareness (e.g., Bartlett, 1932; Haggard & Wolpert, 2005; Head & Holmes, 1911; cf. Simmel, 1966; see Vallar & Papagno, 2003, for a review). Similarly, modification of the body image can have consequences for the awareness of tactile information. An important difference between the two is that the body image has primarily visual characteristics, while the body schema has proprioceptive, tactile, and kinetics aspects (see Haggard & Wolpert, 2005; Head & Holmes, 1911; Holmes & Spence, 2006; Paillard, 1999). The separation between body schema and body image shown in the model only indicates that both systems contribute in different ways to the awareness of touch. From the anatomical and functional point of view, however, body schema and body image cannot be so strongly separated (see Gallagher & Cole, 1995, for a discussion on this point; though see Paillard, 1999, for a double dissociation between patients with impairment to the body schema and to the body image).

According to the neurocognitive model outlined here, whenever neural activity from SI and SII triggers a feedback signal from higher-order spatial representations (involving the temporo-parietal junction), tactile information becomes conscious (e.g., Azañón & Soto-Faraco, 2008; Gallace & Spence, 2008). Without the occurrence of such a feedback signal, tactile information might still affect performance, but it cannot be reported consciously (this might be the case for the implicit processing of tactile stimuli in patients suffering from neglect and/or extinction; e.g., Maravita, 1997; see Gallace & Spence, 2008, for a review; see also Lamme, 2001, 2006, for the suggestion that feedback connections play a crucial role in our awareness of visual information). We believe that a certain threshold level of activation in the circuit needs to be reached, be it a certain rate of neural firing or the oscillation of the circuit at a give frequency (e.g., Palva et al., 2005; VanRullen & Koch, 2003), in order for awareness to be generated (e.g., Blakemore et al., 2005). Back-projections from higher order areas to SI and SII also lead to the awareness of touch, even in the absence of direct stimulation of the somatosensory cortices and of tactile receptors located in the skin. This might be the case, for example, for tactile illusion and hallucinations.

The neural network represented here, which is thought to be involved in the awareness of tactile information, is the same one that is also involved in the processing, selection, and storage of that information (cf. Berti et al., 2005): No areas, other than those involved in tactile information processing, are responsible for the awareness of tactile events. Similarly, the awareness of touch is not related to a particular component of the model, but rather it is embedded into the connections of the model. In particular, the activation of both top-down and bottom-up connections result in the awareness of tactile stimulation (see Jackendoff, 1987).

Finally, one might wonder whether the neural network responsible for the awareness of touch is lateralized in the brain. On the basis of a number of neuropsychological and neuroimaging studies (see Gallace & Spence, 2008, for a recent review), we believe that the awareness of touch is more likely to be compromised when right brain structures are damaged (see also Vallar, 2007). This is mainly due to the fact that those neural systems that are thought to support spatial representations, based on different frames of reference, have been shown to be found in the right hemisphere (e.g., Karnath, Ferber, & Himmelbach, 2001; Vallar, 2001).

Conclusions

The aim of the present literature review has been to highlight the role of those somatosensory brain areas whose activation is critical for an awareness of tactile information to emerge. The studies discussed here have highlighted the fact that early cortices constitute an important part of the neural circuit responsible for our conscious perception of touch. This claim clearly contrasts with the simplistic view that sensory areas such as SI only register and catalogue tactile sensations (see also the recent debate on whether or not V1 activity is necessary for visual awareness; e.g., Kleiser et al., 2001; Rees, 2007). In particular, we have shown that modulation of the activity in SI, by means of multisensory stimulation as well as motor activity, results in important changes in our experiences of touch (e.g., Blakemore et al., 1995). This change also appears to be linked to the way in which we represent our body (e.g., Blakemore et al., 1995; Schaefer et al., 2008).

The present review has also shown that neural activation across the somatosensory cortex by itself cannot account for awareness of information (such as previously reported for V1 area and visual consciousness; see Crick & Koch, 1995). Other brain areas, in particular, those related to the processing of spatial and motor information, seem to be involved in the conscious perception of touch (which act upon SI in a feedback manner). Owing to the hierarchical and serial organization of the somatosensory system, implicit information processing is still possible whenever SI is spared. No access to information occurs after damage to SI. Here, we suggest that the lack of tactile awareness of tactile stimulation likely requires damage to higher order areas, in particular, damage to a complex circuit comprising the parietal and premotor cortex (see also Gallace & Spence, 2008).

This article has reviewed those studies showing that we can be aware of touch even when no peripheral receptors are stimulated. This is the case for different forms of tactile illusions and hallucinations. Even more interesting is the consideration that the conscious localization of tactile sensations can be referred to artificial limbs (even to supernumerary limbs; e.g., Schaefer et al., 2008a) when placed in an anatomically-plausible position. All of these phenomena appear to be determined by top-down effects on the activation of SI, arising at the level of multisensory areas of the brain (see Gallace & Spence, 2008).

These considerations are not only of theoretical but also of applied importance. Fields that would benefit from the study of the neural correlates of tactile awareness include those linked to the rehabilitation of patients who have lost a limb (e.g., Petruzzo et al., 2006) as well as those related to the development of new technologies, such as virtual reality and telemanipulation (see Gallace et al., 2007).

We believe, however, that before any progress towards the rehabilitation of such patients can be made, a greater understanding of the neural correlates of tactile awareness is necessary.

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